2013

Measuring the relative resilience of subarctic lakes to global change: redundancies of functions within and across temporal scales

David G. Angeler
Swedish University of Agricultural Sciences, david.angeler@slu.se

Craig R. Allen
University of Nebraska-Lincoln, callen3@unl.edu

Richard K. Johnson
Swedish University of Agricultural Sciences

50 YEARS WITH IMPACT
Journal of Applied Ecology
1913 2013 British Ecological Society CELEBRATING 100 YEARS

Journal of Applied Ecology 2013, **50,** 572–584 doi: 10.1111/1365-2664.12092

Measuring the relative resilience of subarctic lakes to global change: redundancies of functions within and across temporal scales

David G. Angeler[1]*, Craig R. Allen[2] and Richard K. Johnson[1]

[1]*Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden; and* [2]*U.S. Geological Survey, Nebraska Cooperative Fish and Wildlife Research Unit, School of Natural Resources, University of Nebraska – Lincoln, Lincoln, NE, 68583-0961, USA*

Summary

1. Ecosystems at high altitudes and latitudes are expected to be particularly vulnerable to the effects of global change. We assessed the responses of littoral invertebrate communities to changing abiotic conditions in subarctic Swedish lakes with long-term data (1988–2010) and compared the responses of subarctic lakes with those of more southern, hemiboreal lakes.

2. We used a complex systems approach, based on multivariate time-series modelling, and identified dominant and distinct temporal frequencies in the data; that is, we tracked community change at distinct temporal scales. We determined the distribution of functional feeding groups of invertebrates within and across temporal scales. Within and cross-scale distributions of functions have been considered to confer resilience to ecosystems, despite changing environmental conditions.

3. Two patterns of temporal change within the invertebrate communities were identified that were consistent across the lakes. The first pattern was one of monotonic change associated with changing abiotic lake conditions. The second was one of showing fluctuation patterns largely unrelated to gradual environmental change. Thus, two dominant and distinct temporal frequencies (temporal scales) were present in all lakes analysed.

4. Although the contribution of individual feeding groups varied between subarctic and hemiboreal lakes, they shared overall similar functional attributes (richness, evenness, diversity) and redundancies of functions within and between the observed temporal scales. This highlights similar resilience characteristics in subarctic and hemiboreal lakes.

5. *Synthesis and applications*. The effects of global change can be particularly strong at a single scale in ecosystems. Over time, this can cause monotonic change in communities and eventually lead to a loss of important ecosystem services upon reaching a critical threshold. Dynamics at other spatial or temporal scales can be unrelated to environmental change. The relative 'intactness' of these scales that are unaffected by global change and the persistence of functions at those scales may safeguard the whole system from the potential loss of functions at the scale at which global change impacts can be substantial. Thus, an understanding of scale-specific processes provides managers with a realistic assessment of vulnerabilities and the relative resilience of ecosystems to environmental change. Explicit consideration of 'intact' and 'affected' scales in analyses of global change impacts provides opportunities to tailor more specific management plans.

Key-words: benthic invertebrates, cross-scale resilience, global change, panarchy, time-series modelling, vulnerability

*Correspondence author. E-mail: david.angeler@slu.se

Introduction

There is consensus in the scientific community that current rates of global change are unprecedented (Sala *et al.* 2000). Ecosystems at high latitudes, especially fresh waters including subarctic and arctic lakes, streams, ponds and wetlands, are particularly sensitive to change due to the combined impacts of modified ice cover regimes, increasing water temperature, thawing permafrost and changes to hydrological processes and water balance (Prowse *et al.* 2006; Milner, Brown & Hannah 2009; Vincent *et al.* 2011). In fact, the impact of global change on northern fresh waters is likely to be twice as much as the global average (Walsh *et al.* 2011) and may be having dramatic effects on the abiotic template and biodiversity of freshwater ecosystems (Wrona *et al.* 2006; Prowse *et al.* 2011). These effects can jeopardize many of the important provisioning services that sustain local populations and climate regulation services that are critical to humanity (Reist *et al.* 2006; Huntington, Goodstein & Euskirchen 2012). Awareness of periled northern fresh waters has resulted in calls of internationally standardized biomonitoring efforts to assess and mitigate the impacts of global change on arctic fresh waters and their locally and globally coupled societies (Culp *et al.* 2012). In this study, we analyse unique long-term biomonitoring data to evaluate the vulnerability of subarctic Swedish lakes to changing environmental conditions during the last two decades. We compare temporal dynamics of littoral invertebrate communities in subarctic lakes to lower latitude, hemiboreal lakes, to assess whether vulnerability to environmental change varies between these two climatic zones.

Increasing evidence suggests that ecological structure and dynamics are regulated by a small number of ecological processes (Carpenter & Leavitt 1991; Levin 1992) that operate at characteristic temporal and spatial scales (Holling 1992; Allen *et al.* 2006; Angeler, Drakare & Johnson 2011). A multiscale spatio-temporal view of ecosystems is useful because effects of global change can be scale specific. For instance, community changes can arise from slow changes in average temperature or nutrient deposition rates that act over broad spatial extents and these slow changes can trigger impact on faster-changing processes at local scales, for example, annually recurring nuisance algal blooms (Angeler, Allen & Johnson 2012). Ecologists have developed tools (discontinuity analyses) that allow quantification and comparison of sudden changes in ecological patterns (Allen & Holling 2008). The ability to measure and quantify discontinuities provides insight regarding the number of dominant scales of process and structure that are present in a system (Allen, Gunderson & Johnson 2005; Stow, Allen & Garmestani 2007). Here, we use multivariate time-series modelling to identify temporal structure in long-term data sets; that is, we identify different temporal frequency patterns in the abundance structure of invertebrate communities (Angeler, Viedma & Moreno 2009). Because the method allows tracking temporal variability at decadal, inter- and intra-annual scales, we are able to assess community dynamics at different temporal scales. Thus, scale is used in a temporal context in this study, meaning that dynamics of a community within an ecosystem can unfold at different temporal scales.

Processes in ecosystems, such as primary productivity or the flux of matter and energy, depend on the functional roles of species and the composition of species in functional groups (rather than on species richness), how these functions are distributed within an ecosystem and by their differential responses to disturbances (Hooper & Vitousek 1997; Nyström 2006; Cadotte, Carscadden & Mirotchnick 2011; Pinho *et al.* 2011). Ecologists have begun to explicitly consider the distributions of functions at multiple scales of space and time, because understanding how functions are distributed within and across scales, and positive interactions between functions and processes, has important implications for the resilience of ecosystems (Fischer *et al.* 2007; Wardwell *et al.* 2008; Sundstrom, Allen & Barichievy 2012). More specifically, the resilience of ecological processes, and ultimately of ecosystems, depends in part on the distribution of functions within and across scales (Peterson, Allen & Holling 1998). At either a single spatial or temporal scale, resilience is enhanced by an imbrication of ecological function among species of different functional groups that operate at the same scales (Allen, Gunderson & Johnson 2005). Together with the variation in responses to environmental change by species within a functional group (response diversity; Elmqvist *et al.* 2003; Chillo, Anand & Ojeda 2011), an assessment of within and cross-scale redundancy of functions allows a measure of resilience, from which important management information can be derived (Cadotte 2011).

We focus on the temporal structure of functional metrics of littoral invertebrates, because this group comprises a variety of taxa with different feeding modes (predators, shredders, grazers, gatherer–collectors, filterers) that play a pivotal role in different ecosystem functions in aquatic ecosystems, including secondary production, leaf litter processing, nutrient cycling and matter and energy fluxes (e.g. Wallace & Webster 1996). In addition to functional metrics, we use taxon richness and assess thermal preferences and the Red List status (extinction risk of species assessed by the International Union for Conservation of Nature) of invertebrates for Sweden to gain insight regarding the extent relevant functions are associated with potentially threatened taxa. Our time-series modelling approach permits us both to test whether there are dominant temporal frequencies (or 'temporal scales') of species abundances present, and if so, how many and what frequencies or scales. We can then determine the distribution of functions within and across these temporal scales, to provide a tool to assess resilience. For instance, if a few individuals only represent shredders at one but not at other temporal scales, they are more vulnerable than other functional feeding groups (e.g. predators) that occur with many species within and across temporal scales.

Assessing the scale-specific temporal structure thus has clear relevance for management and conservation, which in the example given above implies that processes related to, for instance, leaf litter decomposition could be compromised. More generally, the effect of a particular global change may be particularly strong at a single temporal scale. However, temporal dynamics at other scales may be unaffected and may rather track other processes (e.g. dispersal among habitats). Thus, an understanding of scale-specific distributions of structural and functional attributes provides managers with an assessment of vulnerabilities to environmental change, especially in identifying 'intact' and 'affected' scales. The identification of affected and intact scales in analyses of global change impacts can then guide specific management targets. Here, we use subarctic lakes with predicted high vulnerability to environmental change as model systems to identify structure in time-series data to identify temporal patterns and use the expectations of the cross-scale resilience model to evaluate their management implications. We compare the patterns found in subarctic lakes to a set of lakes at more southern latitudes to assess whether the subarctic lakes appear more vulnerable to environmental change.

Materials and methods

STUDY AREA

In the late 1980s, Sweden initiated a long-term monitoring programme of multiple habitats and trophic levels of lakes. Eight lakes from the monitoring data were chosen for this study based on the length of time series available (23 years) and their location in contrasting climatic zones. Four lakes were situated in the subarctic (dfc) region according to the Köppen–Geiger climate classification system (Köppen 1936; Peel, Finlayson & McMahon 2007). The other four lakes were located in the hemiboreal climatic (dfb) zone (Appendix S1, Supporting Information). This classification scheme identifies climatic zones as a function of their vegetation characteristics, temperature and precipitation regimes. Samples for environmental variables and littoral invertebrate assemblages used in this study were collected between 1988 and 2010. Information regarding the monitoring programme can be found at: http://www.slu.se/en/faculties/nl/about-the-faculty/departments/department-of-aquatic-sciences-and-assessment/data-host/. Selected environmental variables and the geographical position of these lakes are provided in Appendix S1, Supporting Information.

SAMPLING

Standard sampling and analyses protocols for abiotic and biological variables were used throughout the period of our study. These standard protocols are certified and quality controlled through the Swedish Board for Accreditation and Conformity Assessment (SWEDAC; http://www.swedac.se/en/). Water quality data were obtained from surface water samples (taken at 0·5 m depth^{-1}) that were collected four to eight times each year at a mid-lake station in each lake. Water was collected with a Plexiglas sampler and kept cool during transport to the laboratory. Samples were analysed for variables related to acidity (pH, alkalinity, SO_4^{2-} concentration), nutrients (total P, total N, Ca), water clarity (Secchi disc depth, water colour) and ionic strength (electrical conductivity). All physicochemical analyses were done at the Department of Aquatic Sciences and Assessment following international (ISO) or European (EN) standards when available (Wilander, Johnson & Goedkoop 2003). Measurement intervals and uncertainties for each variable can be found at: http://www.slu.se/en/faculties/nl/about-the-faculty/departments/department-of-aquatic-sciences-and-assessment/laboratories/geochemical-laboratory/water-chemical-analyses/.

Sampling of benthic invertebrates followed Swedish standards throughout the study period (SS-EN 27828). Briefly, invertebrates were collected in each lake from one wind-exposed, vegetation-free littoral habitat in late autumn (end of October–early November in the hemiboreal lakes; end of September in the subarctic lakes to cover similar environmental and climatic conditions) each year. Five replicate samples were taken using standardized kick sampling with a hand net (0·5 mm mesh size). Each sample was taken by disturbing the bottom substratum for 20 s along a 1-m-long stretch of the littoral region at a depth of c. 0·5 m. Samples were preserved in 70% ethanol in the field and processed in the laboratory by sorting against a white background with 10 × magnification. Invertebrates were sorted, identified to the finest taxonomic unit possible and counted using dissecting and light microscopes by the same person, a trained taxonomist, throughout the study, thereby reducing a researcher-based bias in sample evaluation.

STATISTICAL ANALYSES

Revealing patterns of species groups at independent temporal scales

We used multivariate time-series modelling to identify independent frequency patterns of invertebrate community dynamics over the study period (Angeler, Viedma & Moreno 2009) (Fig. S1, Supporting Information). The method is based on redundancy analysis (RDA), where time is modelled with a principal coordinate of neighbour matrices (PCNM) approach. The analysis converts a time vector comprised of 23 time steps (i.e. 23 sampling years of invertebrates between 1988 and 2010) into a series of PCNM variables akin to a Fourier transform (i.e. a number of different sine waves with different frequencies are derived from the linear time vector).

Principal coordinate of neighbour matrices variables are related through a forward selection process to the community data sets by means of RDA. The RDA retains significant PCNM variables, and these are linearly combined to extract temporal patterns in species abundances from the species matrices; that is, the RDA identifies species with similar temporal frequency patterns in the species × time matrix and uses their temporal pattern to calculate a modelled species group trend for these species based on linearly combined PCNM. The significance of the temporal frequency patterns of all modelled species groups revealed by the RDA is tested with permutation tests.

The RDA relates each modelled temporal frequency pattern associated with a species group with a significant canonical axis. The R software generates linear combination (lc) score plots, which display the modelled temporal frequencies of species groups that are associated with each canonical axis. Based on the number of significant canonical axes, the number of modelled

species groups with different temporal frequency patterns can be deduced. The ecological relevance of temporal frequencies is quantified using adjusted R^2 values of the canonical axes. The overall temporal patterns of frequencies present in the whole community can then be deduced from the number of significant canonical axes in the RDA models.

The canonical axes are orthogonal, so the PCNM–RDA approach reveals temporal frequency patterns of species groups that are independent from each other. Because frequency patterns can arise from processes operating at different temporal scales, this method is useful for more accurately assessing the organization of ecological communities from a complex systems perspective (Angeler, Drakare & Johnson 2011). Rather than assessing change in the 'overall' community, we infer patterns of species-group-specific trends with different frequencies that could indicate community organization at different temporal scales.

Our calculations and analyses are based exclusively on an automatic statistical procedure, thereby avoiding potential researcher-induced bias in model construction. Specifically, for all relevant steps in the analysis, including conversion of the linear time vector to PCNM variables and calculation of modelled species group trends to visual presentation of the results in form of lc score plots, we used the 'quickPCNM' function implemented in R 2.15.1 statistical software package (R Development Core Team 2012). Each lake analysis was based on Hellinger-transformed invertebrate abundance data. The Hellinger transformation consists of transforming the abundance data into relative species values per temporal unit, by dividing each species value by the species sum across time steps and then taking the square root of the resulting values. Legendre & Gallagher (2001) have shown that the Hellinger transformation avoids problems when community data are analysed with Euclidean distance-based methods like RDA (Legendre & Gallagher 2001).

Abiotic and biotic correlates of long-term patterns of individual species groups

To identify the environmental correlates of each temporal frequency patterns of invertebrates (i.e. modelled lc scores), we used Spearman rank correlation analyses. Although our approach allows an assessment of species contributions to the temporal frequency patterns through their correlation with significant canonical axes (Angeler, Viedma & Moreno 2009), the significance of these correlations cannot be evaluated. Therefore, we also used Spearman rank correlation analyses to relate the raw abundance data of individual invertebrate taxa with the modelled temporal frequencies. For all analyses, we used taxa that were identified to species and morphotypes that could be classified into functional feeding groups for further analysis. Taxa with higher taxonomic-level resolution (family and above) were not included to not unduly influence the analyses through ambiguous feeding group assignments. Taxa correlating with modelled temporal frequency patterns were classified into filterers, gatherers, grazers, omnivores, shredders and predators based on scores between 1 and 10, with 10 indicating highest feeding preference, using the online data base www.freshwaterecology.info (Schmidt-Kloiber & Hering 2012). Omnivores were comprised of taxa that scored identically among different feeding groups, here typically gatherers and grazers. We also assessed the thermal range preferences (cold stenotherm, warm stenotherm, eurytherm) and the Red List status of the identified taxa for Sweden using the same online data base.

Definition of functional metrics used for the study

Upon classification of invertebrate taxa into feeding groups, we calculated the following functional measures for each temporal frequency of each lake: (i) functional richness as the number of feeding groups present at each temporal frequency (temporal scale), (ii) functional diversity based on the exponentiated Shannon–Wiener index (exp H') (here the number of feeding groups [equivalent to the number of taxa in analysis of community structure] and the number of species that belong to a feeding group [equivalent to the abundance of taxa in analysis of community structure]). Jost (2007) and Tuomisto (2010) demonstrated that exponentiation of H' makes richness and diversity data directly comparable, (iii) Functional evenness (calculated as the quotient between functional diversity and functional richness). This measure makes evenness independent from richness (Tuomisto 2012), thereby not confounding evenness patterns that may arise from a covariation with richness, (iv) Within-scale redundancy (the average number of species within each functional group at each temporal frequency scale; Allen, Gunderson & Johnson 2005) and (v) Cross-scale redundancy (the average number of temporal frequency scales at which each function is represented; Allen, Gunderson & Johnson 2005). In addition to these functional measures, we calculated a structural community metric (taxon richness) for each temporal scale identified.

Statistical comparisons

We used Kendall's tau rank correlations (Kendall 1938), a non-parametric test of concordance, to assess whether water chemistry variables change monotonically through time. This also allows assessment of whether patterns of change differ between environmental variables.

Repeated-measures analyses of variance (rm-ANOVA) was used to compare the temporal frequency patterns of invertebrates between the subarctic and hemiboreal lake groups to contrast the temporal dynamics identified through the multivariate time-series analysis (RDA–PCNM) of the invertebrate species groups between the lake types. The modelled scores (lc scores), representing the temporal frequency pattern identified through RDA, and the water quality variables were compared between lake types (i.e. subarctic vs. hemiboreal). No data transformation of modelled scores was required for fulfilling the assumptions of parametric tests. However, assumptions of sphericity were violated. The degrees of freedom were therefore corrected according to Huynh & Feldt (1976) to obtain accurate significance levels (note that d.f. can be expressed as decimals as a result of this correction procedure). Although the rm-ANOVA reports treatment, time and interaction effects, we consider only the latter relevant in the present study. If the temporal patterns of species groups are similar between subarctic and hemiboreal lakes, then the interaction term will not be significant.

Second, to evaluate whether subarctic lakes are more vulnerable to global change compared to hemiboreal lakes, we used two-way ANOVAS to compare the distribution of the metrics taxon richness, functional richness, functional diversity, functional evenness and average within-scale redundancy between temporal frequency patterns and across lakes. Here, these metrics comprised the dependent variables and lake type (subarctic, hemiboreal; fixed factor) and temporal scale (temporal frequencies associated with RDA 1 and RDA 2, respectively; fixed factor) comprised the independent

variables. We also examined whether within-scale redundancy at each temporal scale and the cross-scale redundancy between these scales vary as a function of lake type and functional feeding group. In this analysis, within-scale redundancy at both temporal scales and the cross-scale redundancy comprised the dependent variables and functional feeding groups the independent variables. When a significant feeding group effect was detected, *a posteriori* comparisons were made using the Tukey's HSD test.

These univariate comparisons were complemented with multivariate analyses using nonmetric multidimensional scaling (NMDS) in Primer 6 (Primer-E Ltd, Plymouth, UK) of Bray–Curtis transformed similarity matrices on square-root-transformed data, to reveal similarity of functional feeding groups between subarctic and hemiboreal lakes at both temporal frequency scales in multivariate ordination space (999 reruns). NMDS was followed by permutational multivariate ANOVA (PERMANOVA) to contrast multivariate invertebrate functional attributes between lake types (subarctic vs. hemiboreal lakes, fixed factor) and temporal scale (RDA 1 vs RDA 2, fixed factor). PERMANOVAS were calculated on Bray–Curtis and Sørensen similarity matrices of square-root-transformed species data (9999 unrestricted permutations of raw data) using PERMANOVA v1.6 (Anderson 2005).

For both univariate and mutivariate comparisons, we consider interaction terms crucial for inference. If the interactions are significant, we conclude that the relative resilience of one lake type, based on the structure and distribution of functions within and across temporal scales, differs significantly from the other lake type. In turn, this indicates that one lake type is potentially more vulnerable to environmental change relative to the other lake type.

Results

TEMPORAL PATTERNS AND TRENDS OF ENVIRONMENTAL VARIABLES

The patterns of temporal change in water quality variables differed between subarctic and hemiboreal lakes (Fig. 1). Variables related to water clarity changed significantly over time in hemiboreal (Secchi transparency: Kendall's tau = −0·84, $P < 0·001$; water colour: Kendall's tau = 0·70, $P < 0·001$) but not in subarctic lakes ($P > 0·05$) (Figs 1a, b). In contrast, variables related to acidity increased significantly over time in subarctic (pH: Kendall's tau = 0·65, $P < 0·001$, alkalinity: Kendall's tau = 0·68, $P < 0·001$) but not in hemiboreal lakes ($P > 0·05$) (Figs 1c, d). Also, anions and cations showed different patterns, with Ca increasing in subarctic (Kendall's tau = 0·68, $P < 0·001$) and decreasing in hemiboreal lakes (Kendall's tau = −0·74, $P < 0·001$) (Fig. 1e); SO_4 decreased monotonically in hemiboreal lakes (Kendall's tau = −0·96, $P < 0·001$), whilst it fluctuated around a long-term mean in subarctic lakes (Fig. 1f). Electrical conductivity, a measure of ionic strength, showed similar patterns as Ca in both lake types (subarctic: Kendall's tau = 0·32, $P = 0·03$; hemiboreal: Kendall's tau = −0·75, $P < 0·001$) (Fig. 1h). Total P decreased monotonically in subarctic (Kendall's tau = −0·54, $P < 0·01$) but not in hemiboreal lakes ($P > 0·05$) (Fig. 1i). Finally, water temperature and total N showed fluctuations around a long-term mean in lakes in both climatic regions (Fig. 1g, j).

TEMPORAL FREQUENCY PATTERNS OF INVERTEBRATES

Analysing invertebrate communities with the RDA–PCNM approach revealed significant temporal patterns in all of the eight lakes between 1988 and 2010. Significant temporal patterns were associated with canonical axes 1 and 2 in the RDA models, indicating that species groups of invertebrates operate at two distinct temporal frequencies or scales. The first frequency pattern explained between 36% and 75% of the adjusted variance across all lakes in the models; the second patterns explained between 22% and 35% of the adjusted variance in all invertebrate communities across lakes.

The first temporal frequency of invertebrate species groups generally showed components of monotonic change combined with sine wave properties in both lake types (Figs 2a–h). These patterns cover temporal dynamics that were associated with environmental change over the 23-year study period (see below). We therefore refer to this first temporal frequency group of invertebrates as 'slow groups' that track these slower changes in the environment. By contrast, the second frequency of species groups showed shorter-term periodicity at roughly 10-year intervals, presumably tracking faster ecological processes; these groups will be referred to as 'faster groups' (Figs 2a–h). Spearman rank correlation analyses revealed that the slow groups in subarctic lakes correlated mainly with changes in pH, electrical conductivity and total P, whilst in hemiboreal lakes, water clarity variables, in addition to ions and total P, were important. Faster groups correlated with total N in subarctic lakes, but in hemiboreal lakes, no consistent correlations with environmental variables were found (Table S1, Supporting Information). Despite this, the lack of a significant treatment × time interaction in the rm-ANOVA indicated that temporal frequency patterns of slow and faster groups were similar between subarctic and hemiboreal lakes (slow groups: $F_{2·46,14·76} = 2·76$, $P = 0·09$; faster groups 2: $F_{2·72,16·34} = 2·2$, $P = 0·13$), highlighting conservative patterns.

TAXONOMIC AND FUNCTIONAL STRUCTURE OF SPECIES GROUPS

From the 170 taxa that correlated significantly with slow and faster groups across the lakes, 49 (29%) were eurytherm, 44 (26%) preferred warmer waters and 72 (42%) could not be assigned a thermal preference. Only 5 (3%) taxa were cold stenotherm (the omnivorous mayfly *Ameletus inopinatus*, shredding stoneflies *Capnia atra*, *Capnia* sp., *Nemoura avicularis* and *Nemoura* sp.); they were found only in subarctic lakes and occurred in both the slow and faster group. None of these taxa are red listed in Sweden.

The analysis of community metrics for the slow and faster groups across lakes revealed that on average, 28 and 25 taxa correlated with the slow group in subarctic and hemiboreal lakes, respectively, whilst on average, 10 and 14

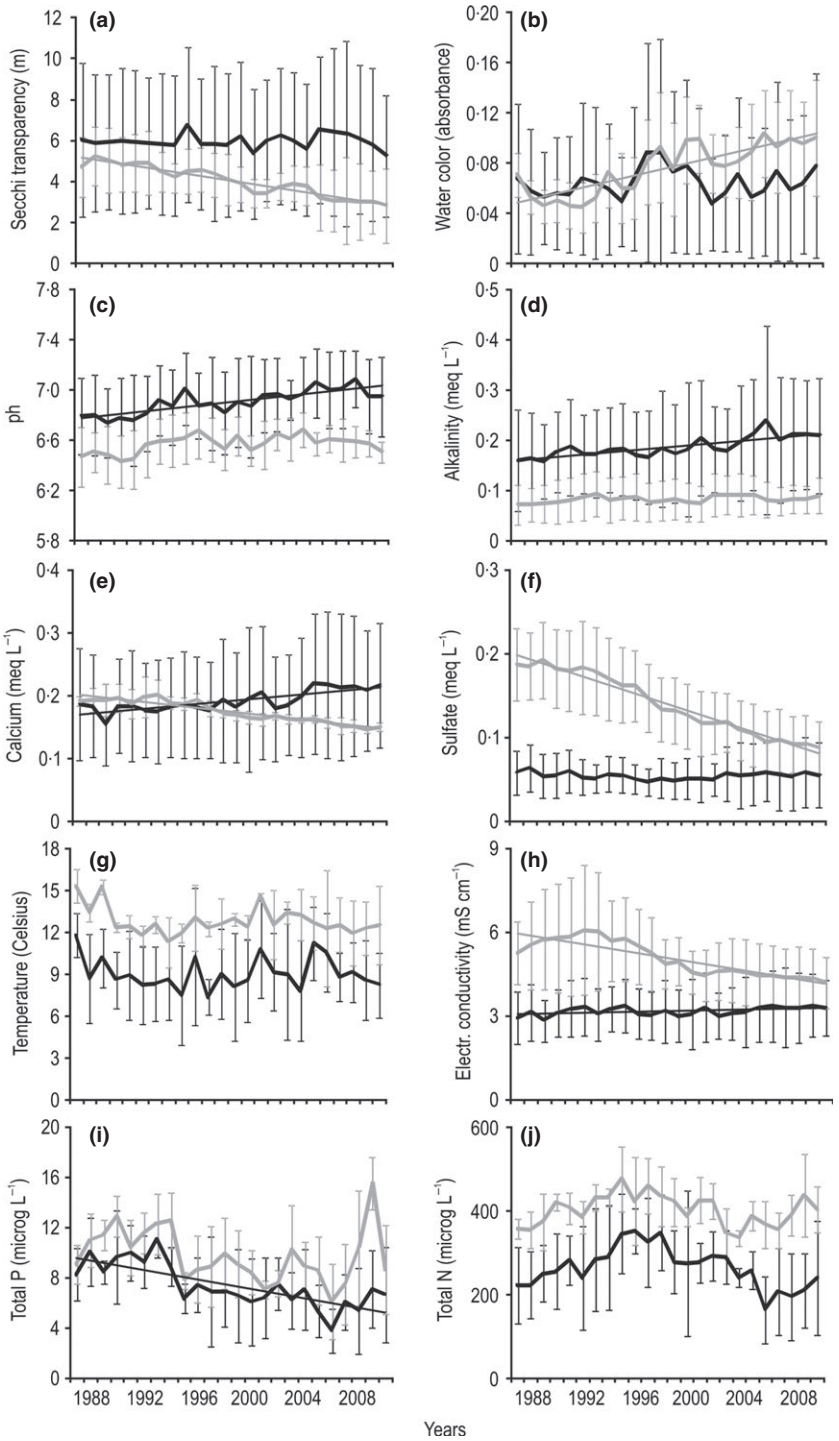

Fig. 1. Temporal patterns of environmental variables in subarctic and hemiboreal lakes. Shown are the means ± standard deviations of four subarctic (black lines) and four hemiboreal (grey lines) lakes. The trend lines indicate significant monotonic change over time revealed by Kendall tau correlation analyses.

species correlated with the faster group in subarctic and hemiboreal lakes, respectively (Fig. 3a). Functional richness, functional diversity and functional evenness showed similar ranges across both species groups and lake types (Figs 3b–d). Because of the higher taxon richness in the slow group, average functional redundancy was also higher for the slow compared to the faster groups in subarctic and hemiboreal lakes (Fig. 3e). Both subarctic and hemiboreal lakes showed similar variability in the patterns of cross-scale redundancy (Fig. 3f). Differences between the two groups responding to their environment at different temporal scales were found only for taxon richness and average within-scale redundancy. Otherwise, no significant effects were detected for lake type or the interaction term in the ANOVAS (Table 1), highlighting that functions are similar in the slow and faster groups of invertebrates in the subarctic and hemiboreal lakes studied here.

Gatherers and predators were the dominant feeding types, with the highest level of functional redundancy in the slow and fast species groups in both lake types, relative to

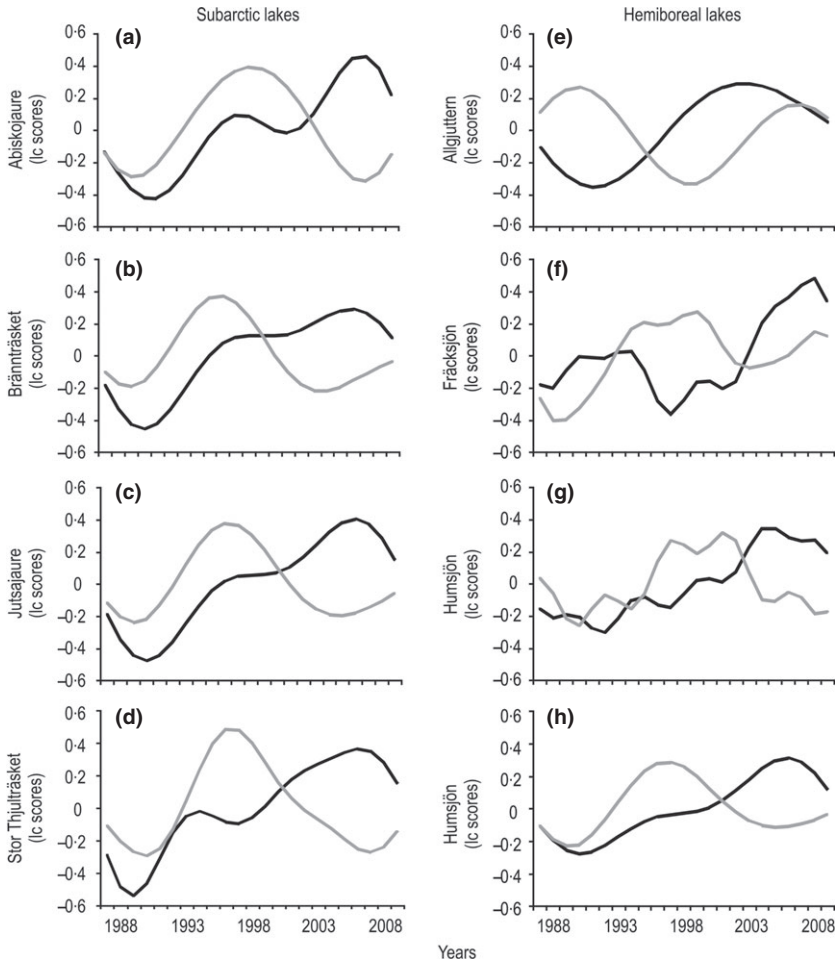

Fig. 2. Temporal patterns of two species groups associated with canonical axis (RDA) 1 ('slow' group; black lines) and RDA 2 ('faster group'; grey lines) obtained from multivariate time-series modelling of invertebrate communities in subarctic (a–d) and hemiboreal (e–h) lakes. Shown are linear combination scores of significant PCNM (principal coordinate of neighbour matrix) variables (see methods for details).

the other feeding groups (Figs 4a–f), and the average redundancy for predators and gatherers was higher than for other feeding groups (slow group: Tukey's HSD test: predators = gatherers > grazers = shredders $\geq$ filterers = omnivores) (faster group: Tukey's HSD test: predators > gatherers = grazers = shredders = filterers = omnivores) (Table 1). However, lake type and interactions were nonsignificant for within-scale redundancy for both groups (Table 1), highlighting similarities between both lake types. Also, the patterns of cross-scale redundancy for each functional feeding group were similar for both lake types (Figs 4g–l), resulting in nonsignificant effects in the ANOVAS (Table 1).

The complementary multivariate analyses are in agreement with the patterns found for univariate metrics. Slow groups of subarctic and hemiboreal lakes clustered, whilst faster groups showed a larger spread in multivariate (NMDS) ordination space (Fig. 5). PERMANOVA based on Bray–Curtis similarities revealed significant differences between lake type and temporal scales, whilst the interaction term was not significant (Table 2). However, PERMANOVA on Sørensen similarity indices, which is only based on presence/absence data, revealed no significant effect, highlighting similar distribution of functions between lake types and scale (Table 2).

Discussion

There is evidence that change in the abiotic environment of Scandinavian lakes and elsewhere is due to the complex interaction of global warming, change in land use and decreasing acid deposition resulting from the implementation of international policy to mitigate the negative ecological effects of anthropogenic acidification (Evans, Monteith & Cooper 2005; Sucker & Krause 2010). Quantitative change, in terms of monotonically changing water quality variables, was evident in the abiotic environment of both lake types, supporting the conjecture that abiotic long-term shifts occur in these lakes. The individual and collective effects of global change are difficult to study mechanistically in correlative long-term studies like ours, but our results show that subarctic and hemiboreal lakes track these changes in qualitatively different ways. Hemiboreal lakes showed consistent decrease in water clarity variables (Secchi depth, water colour) and subarctic lakes an increase in acidity variables (pH, alkalinity). Both lake types also showed distinct temporal patterns of total phosphorus and ions that influenced electrical conductivity. This highlights complex responses to environmental change. Previous studies have shown that decreasing acid deposition leads to the recovery of organic

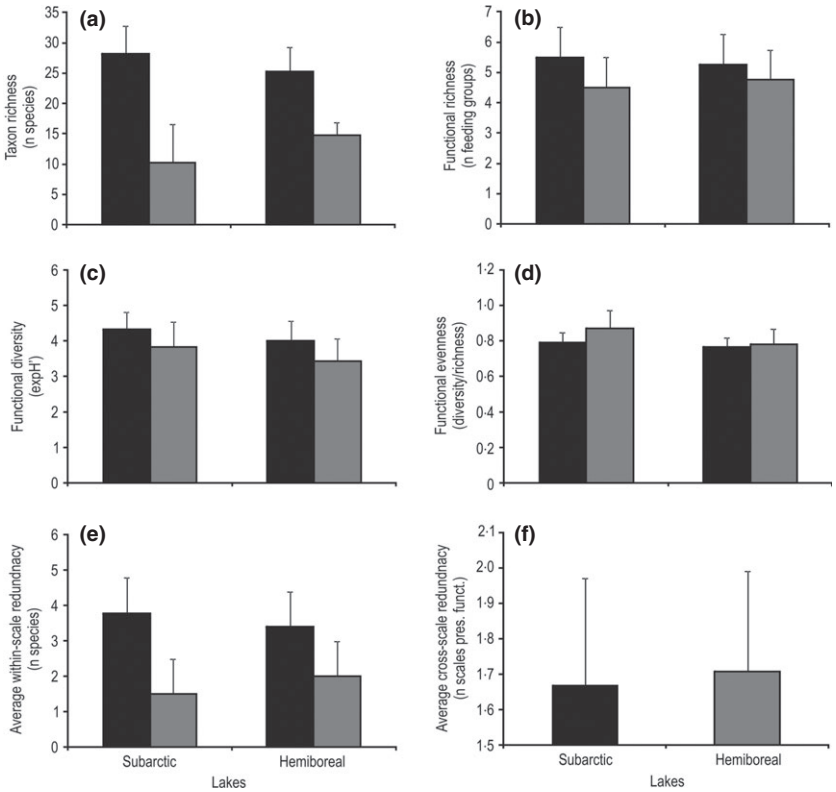

Fig. 3. Comparison of structural (taxon richness; a) and functional (b–d) community metrics and average within-scale redundancy (e) in 'slow' species groups (black bars) and 'faster' species groups (grey bars) for subarctic and hemiboreal lakes. Shown is also the average cross-scale redundancy (the number of scales in which the studied feeding groups are present) for subarctic and hemiboreal lakes (f). Shown are means ± standard deviations of four subarctic and four hemiboreal lakes.

Table 1. Results from ANOVA analyses contrasting effects of lake type (subarctic vs. hemiboreal lakes) and temporal scale ('slow' vs. 'faster' species group) (a) and lake type and feeding groups (predators, shredders, gatherers, grazers, filterers, omnivores) (b) and their interactions, on measures used to assess the relative resilience of lakes

(a)

	Lake type (LT) (d.f. 1, 12)			Scale (S) (d.f. 1, 12)			L × S (d.f. 1, 12)			
	MS	F	*P*	MS	F	*P*	MS	F	*P*	Error
Taxon richness	0·02	1·19	0·30	**0·47**	**25·2**	**<0·001**	0·06	3·17	0·10	0·019
Functional richness	<0·001	0·001	0·97	0·02	1·97	0·19	0·001	0·17	0·69	0·008
Functional diversity	0·007	1·32	0·27	0·02	3·08	0·11	<0·001	0·02	0·89	0·005
Functional evenness	0·004	1·93	0·19	0·002	1·151	0·3	0·001	0·64	0·441	0·002
Within-scale redundancy	0·03	1·12	0·31	**0·22**	**8·95**	**0·011**	0·006	0·24	0·637	0·024

(b)

	Lake type (LT) (d.f. 1, 36)			Feeding group (F) (d.f. 5, 36)			LT × F (d.f. 5, 36)			
	MS	F	*P*	MS	F	*P*	MS	F	*P*	Error
Within-scale redundancy (temporal scale 1)	0·001	0·018	0·90	**0·75**	**19·9**	**< 0·001**	0·03	0·81	0·55	0·038
Within-scale redundancy (temporal scale 2)	0·09	1·43	0·24	**0·24**	**3·65**	**0·009**	0·1	1·49	0·22	0·064
Cross-scale redundancy	0·004	1·042	0·31	0·004	0·938	0·468	0·005	1·17	0·34	0·004

Shown are degrees of freedom (d.f.), mean squares, sources of variation (F-ratios), significance levels and error terms.
Significant effects are highlighted in bold.

carbon concentrations in surface waters to pre-industrial levels (Monteith *et al.* 2007), which suppresses recovery of pH and alkalinity (Erlandsson *et al.* 2010). This may explain the long-term stability of pH and alkalinity and decreasing water clarity observed in hemiboreal lakes. On the other hand, subarctic lakes seem to be more responsive to the direct effects of reduced acid deposition, responding with increases in pH and alkalinity over time. Despite this, water temperature, which is expected to cause increasing thermal stress on arctic biota with global

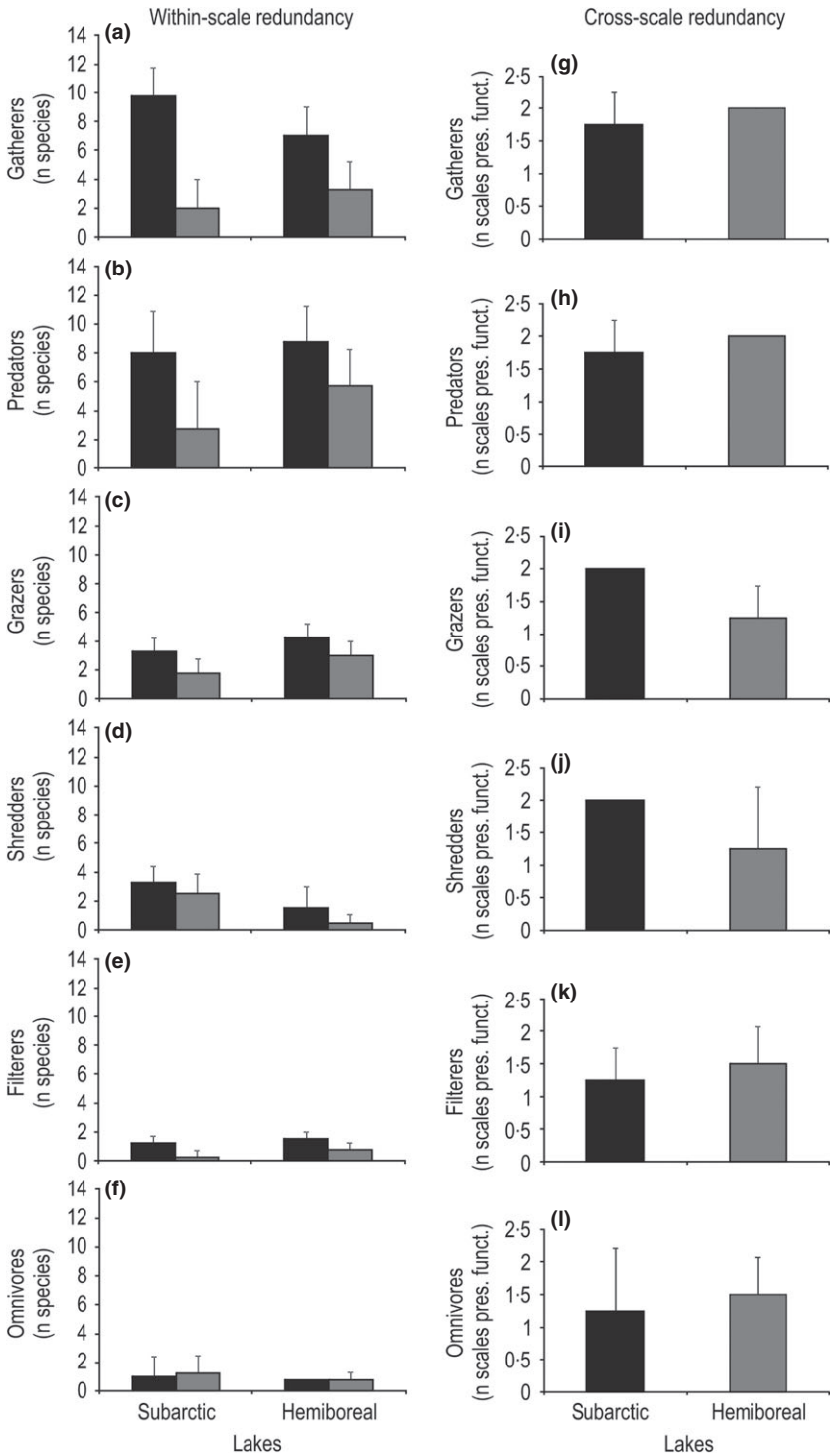

Fig. 4. Patterns of within-scale redundancy for slow (black bars) and faster species groups (grey bars) for gatherers (a), predators (b), grazers (c), shredders (d), filterers (e) and omnivores (f) for subarctic and hemiboreal lakes. Shown are also the cross-scale redundancies for each feeding group in both lake types (g–l).

warming (Walsh *et al.* 2011), fluctuated around a long-term mean rather than increasing monotonically through time. Taken together, our results show that decreasing acidification rather than increasing temperatures indicates different long-term patterns of abiotic change in lakes in both climatic zones. However, our results need careful interpretation because changing temperature regimes are undeniable in northern latitudes (e.g. Walsh *et al.* 2011), and the influence of climatic change on abiotic and biotic lake processes might go undetected when studied with average water temperature alone. Indeed, Johnson & Angeler (2010) have shown that the North Atlantic Winter index well describes the between-year variability in invertebrate community structure. Also, Burgmer, Hillebrand & Pfenninger (2007) have shown that subtle changes in long-term patterns of temperature have had noticeable effects on invertebrate assemblages across Swedish lakes. Thus, multifaceted and indirect effects of global warming, including modified ice cover regimes, thawing permafrost and changes to hydrological processes

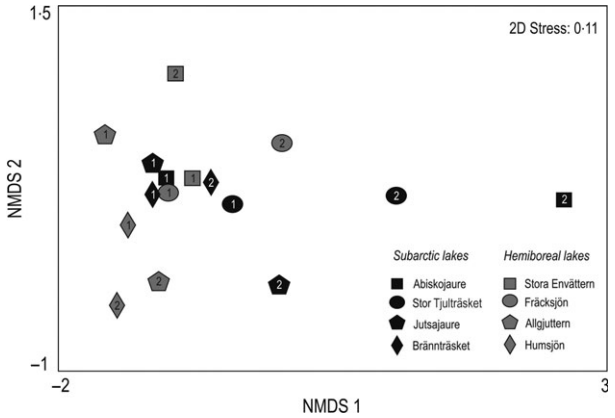

Fig. 5. Nonmetric multidimensional scaling ordination (Bray–Curtis based) showing similarities of functional attributes across slow (symbols with 1) and faster (symbols with 2) species groups in subarctic and hemiboreal lakes.

Table 2. Results of PERMANOVA analysis contrasting multivariate community structure based on Bray–Curtis and Sørensen similarity between lake type (subarctic vs. hemiboreal lakes), temporal scale ('slow' vs. 'fast' species group) and their interactions

Source	d.f.	SS	MS	F	*P* (MC)
Bray–Curtis					
Lake type	**1**	**1580·0**	**1580·0**	**3·866**	**0·0298**
Scale	**1**	**1815·1**	**1815·1**	**4·442**	**0·0190**
Lake type × scale	1	488·4	488·4	1·195	0·3112
Residual	12	4903·8	408·6		
Total	15	8787·2			
Sørensen					
Lake type	1	554·4	554·4	2·219	0·1809
Scale	1	712·2	714·2	2·858	0·1230
Lake type × scale	1	121·2	121·2	0·485	0·5784
Residual	12	2998·7	249·9		
Total	15	4388·6			

Shown are degrees of freedom (d.f.), sums of squares (SS), mean squares (MS), F-ratios (F) and the Monte Carlo asymptotic *P* values (*P* [MC]).
Significant effects are highlighted in bold.

and water balance (Prowse *et al.* 2006; Milner, Brown & Hannah 2009; Vincent *et al.* 2011), would perhaps be more suitable than average water temperature for assessing temperature-related effects on subarctic and hemiboreal lakes.

Despite abiotic long-term change differing quantitatively between subarctic and hemiboreal lakes, the temporal dynamics of invertebrate communities were similar between both lake types. Both groups of lakes consistently showed two distinct groups of species with different temporal patterns. The first group of species showed monotonic patterns of change, whilst the second group of species showed fluctuations. These independent temporal patterns were synchronous across the lakes. This finding is in agreement with previous studies that demonstrated similar patterns of community structure and change in a larger number of lakes across a broad latitudinal gradient (Angeler, Drakare & Johnson 2011; Angeler & Johnson 2012). More generally, these results support theories suggesting the critical importance of spatial and temporal scales in community assembly and resilience (Allen *et al.* 2006; Allen & Holling 2008). Patterns in body mass and the distribution of functions in animal communities have been linked to the relative resilience of ecosystems in the face of global change (e.g. Fischer *et al.* 2007; Wardwell *et al.* 2008; Sundstrom, Allen & Barichievy 2012). However, this is the first use of multivariate time-series modelling, which makes rates of environmental change at distinct temporal scales tractable, to infer relative ecosystem resilience.

We expected that subarctic lakes that are highly vulnerable to global change will exhibit reduced resilience compared to lakes in other climatic regions. However, comparing the distributions of functional metrics within and across temporal scales, a critical component for quantifying the relative resilience in ecosystems (Peterson, Allen & Holling 1998; Allen, Gunderson & Johnson 2005), failed to discern an interaction between lake type (i.e. lakes in contrasting climatic zones) and temporal scale in either the univariate or multivariate analyses. Overall, this suggests that subarctic and hemiboreal lakes have similar functional attributes that characterize their relative resilience through time. This finding is unexpected because subarctic and hemiboreal climatic zones are clearly distinguished on the basis on temperature, vegetation and precipitation patterns (Köppen 1936; Peel, Finlayson & McMahon 2007). Also, invertebrate community composition in the littoral of Swedish lakes has been shown to be contingent on ecoregions that reflect these climatic zones (Johnson 2000; Johnson & Goedkoop 2002). Our results suggest that despite inherent abiotic and biotic differences between subarctic and hemiboreal climates, the distribution of functions in the two species groups associated with different temporal scales is similar. In turn, this suggests both that the observed patterns are conservative and that resilience in both lake types was similar. However, we acknowledge that further research covering a broader range of climate zones (from the Arctic to the Tropics) and temporal frequencies is required to obtain a broader picture of cross-scale linkages and their influence on the resilience of ecosystems facing environmental change.

Despite lakes in both climatic zones sharing similar resilience characteristics, we found scale-inherent patterns and different contributions of functional feeding groups that must be considered for understanding the overall resilience of the studied lakes. Filterers and omnivores had the lowest within-scale redundancy, followed by grazers and shredders. Highest within-scale redundancy was observed for gatherers and predators, although the patterns were contingent on temporal scale (higher in the slow group relative to the faster group). Cross-scale reinforcement was highest for predators and gatherers in hemiboreal lakes and grazers and shredders in subarctic lakes but lowest for filterers and omnivores in both lake types. These findings suggest that the filterers and omnivores are the functional groups most

vulnerable to loss from lakes, and therefore, these groups should be most carefully monitored, as the loss of entire functional groups, or the loss of functional group representation at one or more scales, would have a larger impact on resilience than the loss of species from functional groups with high redundancy. However, we acknowledge that omnivores are polyphagous species and as such should be able to switch from one food source to another. Thus, our results regarding the lower resilience of this feeding group may be counter-intuitive because the ability to switch between food resources can increase their stability in the long term and reduce their vulnerability to environmental change. Gatherers and predators, and shredders and grazers, have the highest redundancy in hemiboreal and subarctic lakes, respectively, and the loss of one or a few species from these functional groups would have relatively minor impact on resilience. Most studies inferring the relative resilience of ecosystems on the basis of cross-scale structure of functions have not studied the contributions of individual functions explicitly. Discriminating between functional groups can help refine the resilience assessment of the overall system and also of contributing individual functions.

The sets of functional traits of assemblages depend on how species are adapted to the environment (Erös *et al.* 2009). There is concern that many cold-stenothermic taxa will be replaced with warm-adapted species in high latitude and altitude fresh waters due to global warming (Vincent *et al.* 2011; Culp *et al.* 2012). The loss of cold-stenothermic species and associated important functions is therefore of special conservation concern (Culp *et al.* 2012). Although we could not assign thermal preferences to 42% of the taxa, but for those that we could, more than 50% tolerated warmer conditions and only 3% were cold stenothermic and occurred only in subarctic lakes. None of the species were red listed in Sweden. This is encouraging because many of the important ecological functions in subarctic and hemiboreal lakes are associated with a majority of species that are already adapted to warmer conditions and currently not recognized as vulnerable to environmental change. This finding also has implications for the longer-term resilience of the lakes. If the majority of functions depend mainly on cold-stenothermic species, unpredictable and potentially catastrophic reorganizations of lakes could arise with the ongoing loss of such species. However, with the temperature preferences for invertebrates observed in this study, and ignoring other factors associated with environmental change, this scenario is unlikely to become reality for the lakes studied here.

MANAGEMENT IMPLICATIONS

Because of the multidimensional and complex organization of ecosystems and communities, their response to management is often highly uncertain (Polasky *et al.* 2011). Patterns within ecosystems that occur across even modestly broad extents and temporal spans are impossible to discern without long-term biomonitoring efforts. Long-term data series, combined with a complex systems approach, allowed us to track community change and gain mechanistic insights into the vulnerability of lake communities to environmental change. Invertebrates in subarctic lakes, one of the most threatened ecosystem types in the face of current global change, organize around distinct temporal frequencies or scaling regimes. Evaluating how functional traits that are relevant for maintaining several ecosystem processes (e.g. secondary production, leaf litter processing, nutrient cycling and matter and energy fluxes) are distributed within and across these temporal scales, we found that putatively severely threatened ecosystems share similar resilience characteristics with lakes in other climatic regions and identified functional groups that should be a focus of monitoring. In and of itself, the identity of the dominant temporal frequencies in a system is critical, because it allows us to separate patterns of cyclic change from stochastic noise.

Researchers have mainly assessed responses of 'whole' communities to broad-scale environmental change, but our study demonstrates that the footprints of changing abiotic conditions in lakes are detectable only in specific groups of species undergoing monotonic change over time. Monotonic community change associated with broad-scale environmental change is a double-edged sword because it is difficult to mitigate or reverse such changes and because it indicates that ecosystems may experience catastrophic regime shifts, with consequent losses of important ecosystem goods and services, when a critical threshold is crossed. Our study suggests that targeting processes acting at temporal scales that are unrelated to broad-scale environmental change has strong management and conservation potential. For example, the subarctic and hemiboreal lakes studied here showed dynamics of a 'faster' species group that were almost unrelated to monotonically changing environmental variables. Although we were unable to identify the mechanisms driving the temporal patterns of these fast species groups in this study, the identification of patterns itself can be of broader utility for management. Management that reinforces functions at specific scales when interventions at other scales are not feasible can strengthen cross-scale linkages and help systems stave off thresholds and collapse. The subarctic and hemiboreal lakes studied here provide a practical example. Taxonomic diversity and redundancy of functions were higher in species groups undergoing slow monotonic change. Functions associated with filterers and omnivores had low within- and cross-scale redundancy. It is uncertain whether these configurations will be maintained as communities continue to track environmental change at this scale. Management that reinforces structures and increases the redundancies of functions at other scales is one way to cope with this uncertainty and assure system resilience despite ongoing environmental change.

In summary, an understanding of scale-specific processes provides managers with a more realistic assessment of vulnerabilities to environmental change. More

importantly, scales that are unaffected by global change may maintain the organization of a system in the face of global change, in effect 'rescuing' ecosystems from ongoing environmental change and potential collapse. The ability to identify vulnerable and intact scales in analyses of global change provides opportunities for improved management.

Acknowledgements

The Swedish Environmental Protection Agency and the many people involved in the monitoring programme for making the analyses of these data sets possible are gratefully acknowledged. This work was supported by the REFRESH (Adaptive Strategies to Mitigate the Impacts of Climate Change on European Freshwater Ecosystems, contract No. 244121, www.refresh.ucl.ac.uk/) project funded by the European Union under the 7th Framework Programme, Theme 6 (Environment including Climate Change) and the August T. Larsson Foundation of the Faculty of Natural Resources and Agricultural Sciences at the Swedish University of Agricultural Sciences. Additional funding from the Swedish Environmental Protection Agency and the USGS John Wesley Powell Center for Analysis and Synthesis is acknowledged. The Nebraska Cooperative Fish and Wildlife Research Unit is jointly supported by a cooperative agreement between the U.S. Geological Survey, the Nebraska Game and Parks Commission, the University of Nebraska–Lincoln, the U.S. Fish and Wildlife Service and the Wildlife Management Institute. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The manuscript was improved by the constructive criticism of two anonymous reviewers.

References

Allen, C.R., Gunderson, L. & Johnson, A.R. (2005) The use of discontinuities and functional groups to assess relative resilience in complex systems. *Ecosystems*, **8**, 958–966.

Allen, C.R. & Holling, C.S. (2008) *Discontinuities in Ecosystems and Other Complex Systems*. Columbia University Press, New York, New York, USA.

Allen, C.R., Garmestani, A.S., Havlicek, T.D., Marquet, P.A., Peterson, G.D., Restrepo, C., Stow, C.A. & Weeks, B.E. (2006) Patterns in body mass distributions: sifting among alternative hypotheses. *Ecology Letters*, **9**, 630–643.

Anderson, M.J. (2005) *PERMANOVA: a FORTRAN Computer Program for Permutational Multivariate Analysis of Variance*. Department of Statistics, University of Auckland, New Zealand. Available at: http://www.stat.auckland.ac.nz/~mja/Programs.htm#Mine.

Angeler, D.G., Allen, C.R. & Johnson, R.K. (2012) Insight on invasions and resilience derived from spatiotemporal discontinuities of biomass at local and regional scales. *Ecology & Society*, **17**, 32. Available at http://www.ecologyandsociety.org/vol17/iss2/art32/

Angeler, D.G., Drakare, S. & Johnson, R.K. (2011) Revealing the organization of complex adaptive systems using multivariate time series modeling. *Ecology & Society*, **16**, 5. Available at http://dx.doi.org/10.5751/ES-04175-160305.

Angeler, D.G. & Johnson, R.K. (2012) Temporal scales and patterns of invertebrate biodiversity dynamics in boreal lakes recovering from acidification. *Ecological Applications*, **22**, 1172–1186.

Angeler, D.G., Viedma, O. & Moreno, J.M. (2009) Statistical performance and information content of time lag analysis and redundancy analysis in time series modeling. *Ecology*, **90**, 3245–3257.

Burgmer, T., Hillebrand, H. & Pfenninger, M. (2007) Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. *Oecologia*, **151**, 93–103.

Cadotte, M.W. (2011) The new diversity: management gains through insights into the functional diversity of communities. *Journal of Applied Ecology*, **48**, 1067–1069.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087.

Carpenter, S.R. & Leavitt, P.R. (1991) Temporal variation in paleolimnological record arising from a trophic cascade. *Ecology*, **72**, 277–285.

Chillo, V., Anand, M. & Ojeda, R.A. (2011) Assessing the use of functional diversity as a measure of ecological resilience in arid rangelands. *Ecosystems*, **14**, 1168–1177.

Culp, J.M., Lento, J., Goedkoop, W., Power, M., Rautio, M., Christoffersen, K.S., Gudbergsson, G., Lau, D., Liljaniemi, P., Sandøy, S. & Svoboda, M. (2012) Developing a circumpolar monitoring framework for Arctic freshwater biodiversity. *Biodiversity*, **13**, 215–227.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtson, J., Walker, B. & Norberg, J. (2003) Response diversity, ecosystem change and resilience. *Frontiers in Ecology and the Environment*, **1**, 488–494.

Erlandsson, M., Cory, N., Köhler, S. & Bishop, K. (2010) Direct and indirect effects of increasing dissolved organic carbon levels on pH in lakes recovering from acidification. *Journal of Geophysical Research*, **115**, G03004, doi:10.1029/2009JG001082

Erös, T., Heino, J., Schmera, D. & Rask, M. (2009) Characterising functional trait diversity and trait–environment relationships in fish assemblages of boreal lakes. *Freshwater Biology*, **54**, 1788–1803.

Evans, C.D., Monteith, D.T. & Cooper, D.M. (2005) Long-term increases in surface water dissolved organic carbon: observations, possible causes and environmental impacts. *Environmental Pollution*, **137**, 55–71.

Fischer, J., Lindenmeyer, D.B., Blomberg, S.P., Montague-Drake, R., Felton, A. & Stein, J.A. (2007) Functional richness and relative resilience of bird communities in regions with different land use intensities. *Ecosystems*, **10**, 964–974.

Holling, C.S. (1992) Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs*, **62**, 447–502.

Hooper, D. & Vitousek, P.M. (1997) The effects of plant composition and diversity on ecosystem processes. *Science*, **277**, 1302–1305.

Huntington, H.P., Goodstein, E. & Euskirchen, E. (2012) Towards a tipping point in responding to change: rising costs, fewer options for Arctic and global societies. *Ambio*, **41**, 66–74.

Huynh, H. & Feldt, L.S. (1976) Estimation of the Box correction for degrees of freedom from sample data in the randomized block and split plot design. *Journal of Educational and Behavioral Statistics*, **1**, 69–82.

Johnson, R.K. (2000) Spatial congruence between ecoregions and littoral macroinvertebrate assemblages. *Journal of the North American Benthological Society*, **19**, 475–486.

Johnson, R.K. & Angeler, D.G. (2010) Tracing recovery under changing climate: response of phytoplankton and invertebrate assemblages to decreased acidification. *Journal of the North American Benthological Society*, **29**, 1472–1490.

Johnson, R.K. & Goedkoop, W. (2002) Littoral macroinvertebrate communities: spatial scale and ecological relationships. *Freshwater Biology*, **47**, 1840–1854.

Jost, L. (2007) Partitioning diversity into independent alpha and beta components. *Ecology*, **88**, 2427–2439.

Kendall, M. (1938) A new measure of rank correlation. *Biometrika*, **30**, 81–89.

Köppen, W. (1936) Das geographische System der Klimate. *Handbuch der Klimatologie*, (eds W. Köppen & G. Geiger), pp. 1–44. Gebrüder Borntraeger, Stuttgart.

Legendre, P. & Gallagher, E.D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271–280.

Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.

Milner, A.M., Brown, L.E. & Hannah, D.M. (2009) Hydroecological response of river systems to shrinking glaciers. *Hydrological Processes*, **23**, 62–77.

Monteith, D.T., Stoddard, J.L., Evans, C.D., De Wit, H.A., Forsius, M., Høgåsen, T., Wilander, A., Skjelkvåle, B.L., Jeffries, D.S., Vuorenmaa, J., Keller, B., Kopácek, J. & Vesely, J. (2007) Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature*, **450**, 537–541.

Nyström, M. (2006) Redundancy and response diversity of functional groups: implications for the resilience of coral reefs. *Ambio*, **35**, 30–35.

Peel, M.C., Finlayson, B.L. & McMahon, T.A. (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, **11**, 1633–1644.

Peterson, G.D., Allen, C.R. & Holling, C.S. (1998) Ecological resilience, biodiversity, and scale. *Ecosystems*, **1**, 6–18.

Pinho, P., Dias, T., Cruz, C., Sim Tang, Y., Sutton, M.A., Martins-Loução, M.-A., Máguas, C. & Branquinho, C. (2011) Using lichen functional diversity to assess the effects of atmospheric ammonia in Mediterranean woodlands. *Journal of Applied Ecology*, **48**, 1107–1116.

Polasky, S., Carpenter, S.R., Folke, C. & Keller, N. (2011) Decision-making under great uncertainty: environmental management in an era of global change. *Trends in Ecology & Evolution*, **26**, 398–404.

Prowse, T.D., Wrona, F.J., Reist, J.D., Hobbie, J.E., Lévesque, L.M.J. & Vincent, W.F. (2006) General features of the Arctic relevant to climate change in freshwater ecosystems. *Ambio*, **35**, 330–338.

Prowse, T., Alfredsen, K., Beltaos, S., Bonsal, B.R., Bowden, W.B., Duguay, C.R., Korhola, A., McNamara, J., Vincent, W.F., Vuglinsky, V., Anthony, K.M.W. & Weyhenmeyer, G.A. (2011) Effects of changes in Arctic lake and river ice. *Ambio*, **40**, 63–74.

R Development Core Team (2012) *R: A language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available at http://cran.r-project.org.

Reist, J.D., Wrona, F.J., Prowse, T.D., Power, M., Dempson, J.B., Beamish, R.J., King, J.R., Carmichael, T.J. & Sawatzky, C.D. (2006) General effects of climate change on Arctic fishes and fish populations. *Ambio*, **35**, 370–380.

Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfeld, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.A. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1170–1774.

Schmidt-Kloiber, A. & Hering, D. (eds.) (2012) www.freshwaterecology.info - the taxa and autecology database for freshwater organisms, version 5.0.

Stow, C., Allen, C.R. & Garmestani, A.S. (2007) Evaluating discontinuities in complex systems: toward quantitative measures of resilience. *Ecology & Society*, **12**, 26. Available at http://www.ecologyandsociety.org/voll2/issl/art26/

Sucker, C. & Krause, K. (2010) Increasing dissolved organic carbon concentrations in freshwaters: what is the actual driver?. *iForest-Biogeosciences and Forestry*, **3**, 106–108.

Sundstrom, S.M., Allen, C.R. & Barichievy, C. (2012) Species, functional groups, and thresholds in ecological resilience. *Conservation Biology*, **26**, 305–314.

Tuomisto, H. (2010) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, **33**, 2–22.

Tuomisto, H. (2012) An updated consumer's guide to evenness and related indices. *Oikos*, **121**, 1203–1218.

Vincent, W.F., Callaghan, T.V., Dahl-Jensen, D., Johansson, M., Kovacs, K.M., Michel, C., Prowse, T., Reist, J.D. & Sharp, M. (2011) Ecological implications of changes in the Arctic cryosphere. *Ambio*, **40**, 87–99.

Wallace, J.B. & Webster, J.R. (1996) The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology*, **41**, 115–139.

Walsh, J.E., Overland, J.E., Groisman, P.Y. & Rudolf, B. (2011) Ongoing climate change in the Arctic. *Ambio*, **40**, 6–16.

Wardwell, D.A., Allen, C.R., Peterson, G.D. & Tyre, A.J. (2008) A test of the cross-scale resilience model: functional richness in Mediterranean-climate ecosystems. *Ecological Complexity*, **5**, 165–182.

Wilander, A., Johnson, R.K. & Goedkoop, W. (2003) *Riksinventering 2000*. En synoptisk studie av vattenkemi och bottenfauna i svenska sjöar och vattendrag. Institutionen för Miljöanalys, Uppsala, Sweden.

Wrona, F.J., Prowse, T.D., Reist, J.D., Hobbie, J.E., Lévesque, L.M.J. & Vincent, W.F. (2006) Climate change effects on aquatic biota, ecosystem structure and function. *Ambio*, **35**, 359–369.

Received 25 October 2012; accepted 14 March 2013
Handling Editor: Marc Cadotte

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Map of Sweden indicating lake position and table with their water quality.

Fig. S1. Flow chart outlining the steps involved in RDA-PCNM time series modelling.

Table S1. Results from Spearman rank correlation analyses.